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Inner tooth morphology of *Homo erectus* from Zhoukoudian. New evidence from an old collection housed at Uppsala University, Sweden

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ABSTRACT

Locality 1, in the Lower Cave of the Zhoukoudian cave complex, China, is one of the most important Middle Pleistocene paleoanthropological and archaeological sites worldwide, with the remains of c. 45 *Homo erectus* individuals, 98 mammalian taxa, and thousands of lithic tools recovered. Most of the material collected before World War II was lost. However, besides two postcranial elements rediscovered in China in 1951, four human permanent teeth from the 'Dragon Bone Hill,' collected by O. Zdansky between 1921 and 1923, were at the time brought to the Paleontological Institute of Uppsala University, Sweden, where they are still stored. This small sample consists of an upper canine (PMU 25719), an upper third molar (PMU M3550), a lower third premolar crown (PMU M3549), and a lower fourth premolar (PMU M3887). Some researchers have noted the existence of morpho-dimensional differences between the Zhoukoudian and the *H. erectus* dental assemblage from Sangiran, Java. However, compared to its chrono-geographical distribution, the Early to Middle Pleistocene dental material currently forming the Chinese-Indonesian *H. erectus* hypodigm is quantitatively meager and still poorly characterized for the extent of its endostructural variation. We used micro-focus X-ray tomography techniques of virtual imaging coupled with geometric morphometrics for comparatively investigating the endostructural conformation (tissue proportions, enamel thickness distribution, enamel-dentine junction morphology, pulp cavity shape) of the four specimens stored in Uppsala, all previously reported for their outer features. The results suggest the existence of time-related differences between continental and insular Southeast Asian dental assemblages, the Middle Pleistocene Chinese teeth apparently retaining an inner signature closer to the likely primitive condition represented by the Early Pleistocene remains from Java, while the Indonesian stock evolved toward tooth structural simplification.

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1. Introduction

1.1. The cave complex site of Zhoukoudian

The karstic cave complex site of Zhoukoudian, approximately 42 km South of Beijing, China, is one of the historically most prolific and extensively investigated prehistoric sites in Asia (e.g., Black et al., 1933; Black, 1934; Weidenreich, 1937, 1941, 1943; Pei and Zhang, 1985; Wu et al., 1985; Zhou et al., 2000; Shen et al., 2001, 2009; Boaz et al., 2004; Gaboardi et al., 2005). Initial excavations were carried out by the paleontologist Otto Zdansky, who unearthed the first human remains of the so-called 'Dragon Bone Hill,' together with faunal material and lithic industry (Zdansky, 1926). Due to the large amount of material recovered at Locality 1, in the Lower Cave (c. 45 human individuals, 98 mammalian taxa, and thousands of lithic tools), Zhoukoudian is considered one of the most important Middle Pleistocene paleoanthropological and archaeological sites worldwide (Wood, 2015).

Zhoukoudian Locality 1 preserves an approximately 40 m thick sedimentary sequence that can be divided, from top to bottom, into 17 stratigraphic levels (Layers), the first top layer being the youngest (Wu et al., 1985; for a review of the stratigraphic sequence, see; Shen et al., 2009). Most of the human remains derive from Layers 8–9 and 3–4 (Yang et al., 1985). The Layers 8 and 9, representing an accumulation of c. 6 m, are composed of limestone and dolomitic rockfall debris interbedded with fine silt/clay and sand (Goldberg et al., 2001). The c. 8 m thick Layers 3 and 4 show various facies: Layer 4 exhibits a succession of fine silts with some clay and sand rich in phytoliths mixed with ashes (with burnt bones suggesting the intentional use of fire; Binford and Ho, 1985; Weiner et al., 1998, 1999; Zhang et al., 2014; Zhong et al., 2014; but see also Wu, 1999), whereas Layer 3 displays centimeter thick cemented beds and localized areas rich in circular voids (vesicles), indicating the presence of vegetation. These features indicate that conditions were becoming progressively wetter during the deposition of Layers 4 and 3, with various long-term openings of the cave (Goldberg et al., 2001).

Based on multiple relative (biostratigraphy, paleomagnetism) and absolute (fission track, thermoluminescence, ESR, ^{230}Th/^{234}U and U-series) dating methods, Layers 8–9 were first estimated to c. 350–500 ka (Zhao et al., 1985; Huang et al., 1993), whereas Layers 3–4 were estimated to c. 250–350 ka (Yuan and Chen, 1980; Pei, 1985; Zhao et al., 1985; Guo et al., 1991; Huang et al., 1993; Grün et al., 1997). More recent analyses based on cosmogenic ^{26}Al/^{10}Be burial dating of quartz sediments and artifacts from the lower strata of Locality 1 yielded ages between 0.68 and 0.78 Ma ago, compatible with the Chinese loess stratigraphy S6–S7 levels and with the MIS 17–19 stages (Shen et al., 2009). These dates, older than previous estimates, indicate that a human presence at northern China latitudes occurred under different climatic and environmental conditions, even during the relatively mild glacial period corresponding to MIS 18 (Shen et al., 2009).

The mammalian assemblages from Layers 8–9 support such interpretation, with a cold-climate fauna suggesting steppe and forest environments and a trend over time toward increasing grasslands, even though warmer climatic conditions prevailed during the deposition of Layer 5 (Shen et al., 2009). Oxygen isotope data from herbivorous teeth from Layers 8–9 and Layer 4 indicate a habitat of mixed C_3/C_4 vegetation and winter monsoon strengthening during the colder, drier intervals (Gaboardi et al., 2005).

The faunal record from Zhoukoudian Locality 1 is rich in invertebrates (fluvial and terrestrial gastropods; Black, 1933), amphibians (at least two anuran taxa; Black, 1933), reptiles (including squamate taxa belonging to Ophidia and Lacertilia, as well as testudines; Black, 1933), and birds (represented by a rich avifauna, including large flightless birds like *Struthio* sp.; Black, 1934; Rich et al., 1986). The mammal fauna is represented by a few Early Pleistocene survivors (like *Equus sanmeniensis*, *Sus lydekkeri* or *Paracamelus gigas*), as well as by a number of taxa recorded for the first time at the regional scale (such as *Myospalax*, *Ursus spelaeus*, *Vulpes vulpes*, *Crocuta ultima*, *Cervus canadensis*; Lucas, 2001; Li et al., 2014). In this respect, it has been estimated that 89% of the fossil taxa represented in this locality are still living today (Lucas, 2001).

Also, the hominin-bearing Layers 8–9 recorded a diversity of large mammals, including non-human primates (*Macaca robustus*), Carnivora (*Canis lupus*, *Ursus thibetanus*, *Ursus arctos*), Perissodactyla (*Dicerorhinus choukoutienensis*, *Coelodonta antiquitatis*, *E. sanmeniensis*), Artiodactyla (*Moschus moschiferus*, *Megaceros pachyosteus*, *Ovis* sp., *Bison* sp.), and Proboscidea (*Palaeoloxodon* cf. *namadicus*), as well as micromammal taxa belonging to Chiroptera (*Rhinolophus*, *Miniopterus*, *Ia*), Lagomorpha (*Ochotona*), Rodentia (*Cricetinus*, *Cricetulus*, *Micromys*, *Rattus*, *Gerbillus*, *Microtus*), and Soricomorpha (*Scaptochirus*, *Neomys*, *Crocidura*; Hu, 1985; Lin, 1985; Yang et al., 1985; Li et al., 2014).

A similar faunal spectrum is found in Layers 3–4, which also contains some additional taxa (notably, Carnivora like *Canis cyonids*, *Nyctereutes sinensis*, *Cuon antiquus*, *Vulpes* cf. *corsac*, *Meles* cf. *leucurus*, *Gulo* sp., *Pachycrocuta brevirostris*, *Machairodus inexpectatus*, *Panthera* cf. *tigris*, *Panthera* cf. *pardus*, *Felis teilhardi*, *Felis* cf. *microtis*, but also Artiodactyla like *Cervus* cf. *nippon*, *Spirocerus peii*, *Bubalus teilhardi*, and Rodentia such as *Trogontherium cuvieri* and *Hystrix* cf. *subcristata*; Hu, 1985; Lin, 1985; Yang et al., 1985; Li et al., 2014). Considering that the majority of these mammals are accustomed to warm-mild climate open grassland, but that some are woodland-associated taxa, the paleoenvironmental and paleoecological signals point to the presence of both expanded steppe and temperate forest during the human occupation phases (Li et al., 2014).

Over 17,000 stone artifacts were recovered in most of the stratigraphic levels of Locality 1, from Layer 11 to 1 (Pei and Zhang, 1985; Wu et al., 1985). Among those, nearly half were classified into 10 morphological categories, where flakes, choppers, core-tools, scrapers, points, and burins are the most abundant (Shen et al., 2016). The assemblage from Layers 4–5 is the largest one. The amount of large size tools tends to decrease from Layers 8–10 to 1–5, while the opposite is true for the flakes and the pointed tools (Wu et al., 1985; Shen et al., 2016). In most layers, the most abundant raw material is quartzite (representing up to 95.8% of the lithic artifacts in Layers 4–5; Li, 2016), a material anyhow not found in the vicinity of the Zhoukoudian area (Pei and Zhang, 1985); on the other hand, the local raw materials, like chert, were mostly exploited during the deposition of Layers 1–5 (Shen et al., 2016).

1.2. Human remains from Locality 1 and the tooth specimens stored at Uppsala University

Zhoukoudian Locality 1 yielded all of the early Middle Pleistocene human remains of the 'Dragon Bone Hill.' Taphonomic analyses show that 67% of such remains exhibit large carnivore bite marks and high bone fragmentation patterns compatible with the activity recorded for the large Pleistocene cave hyena, *P. brevirostris* (Ciochon et al., 2000; Boaz et al., 2000, 2004). Overall, the contextual evidence from the fossil assemblages, the carnivore damage on the bone remains, and the anthropic activity patterns at Zhoukoudian Locality 1 support a scenario of sporadic phases of human occupation, when the cave was not a hyena den (Boaz et al., 2004).

Between 1921 and 1923, four isolated permanent teeth were recovered by O. Zdansky and then brought to the Paleontological